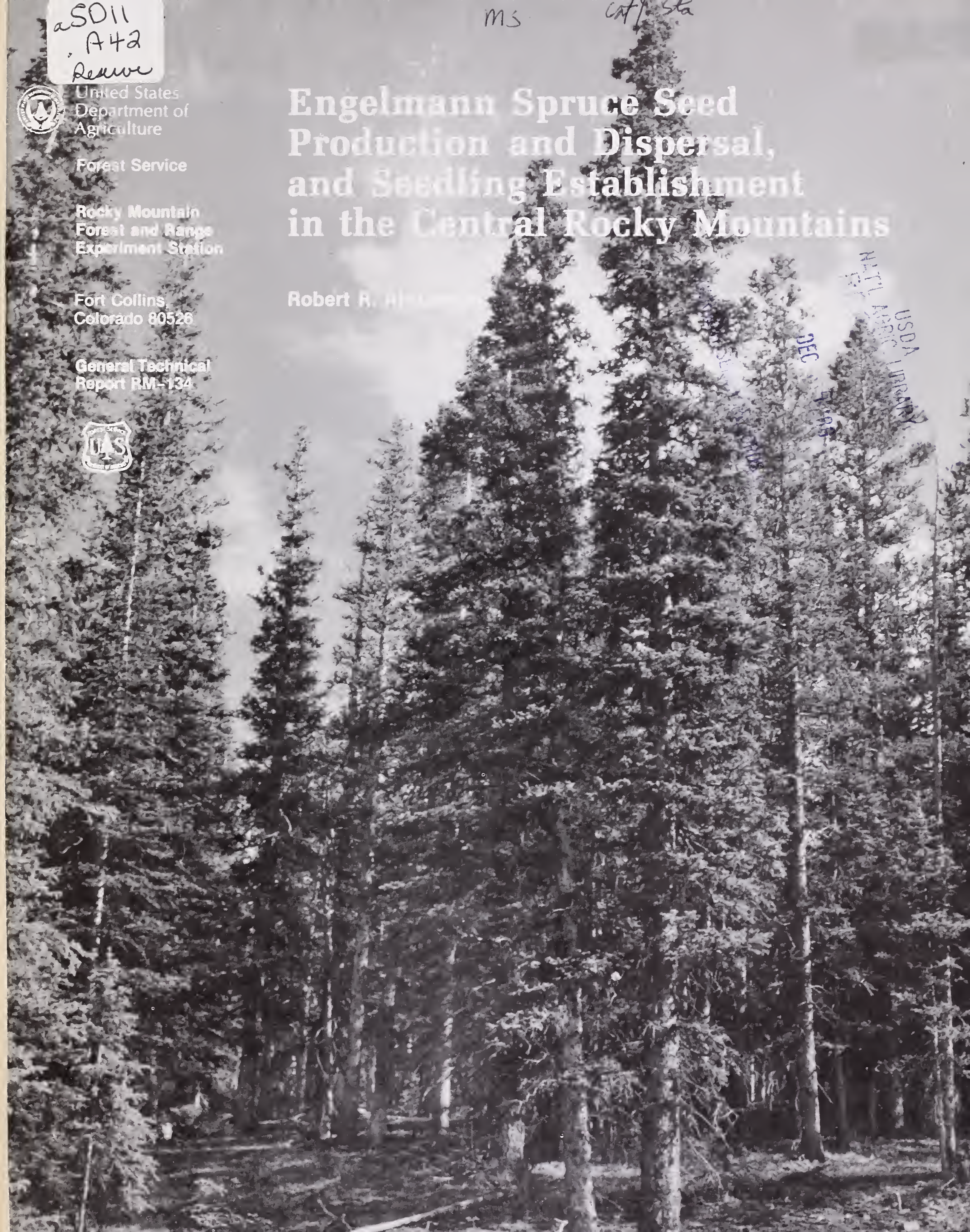

United States
Department of
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Forest Service

Rocky Mountain
Forest and Range
Experiment Station

Fort Collins,
Colorado 80526

General Technical
Report RM-134

Engelmann Spruce Seed Production and Dispersal, and Seedling Establishment in the Central Rocky Mountains

Robert R.

Abstract

Engelmann spruce seed production and dispersal, and seedling establishment in the central Rocky Mountains indicate that in the *Abies lasiocarpa/Vaccinium scoparium* habitat type, shaded, mechanically scarified, mineral soil seedbeds on north aspects can be adequately restocked naturally within a 5-year period in clearcut openings 300 to 450 feet wide. With shade or scarification alone, size of opening that will restock is reduced to 200 to 350 feet. The effective seeding distance is so limited on unshaded natural seedbeds on north aspects and on south aspects regardless of the seedbed conditions that the expectation of natural restocking in a reasonable period of time with clearcutting, is not a realistic option.

Cover Photo.—Old-growth Engelmann spruce-subalpine fir, Fraser Experimental Forest, Colorado.

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Engelmann Spruce Seed Production and Dispersal, and Seedling Establishment in the Central Rocky Mountains

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Contents

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Robert R. Alexander

Prompt establishment of Engelmann spruce (*Picea engelmannii* Parry ex. Engel.) natural reproduction following clearcutting is a major objective in the management of spruce-subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests in the central Rocky Mountains (Alexander 1974, 1977). Engelmann spruce is the most valuable timber species of the type and research and management efforts are directed toward perpetuating it. However, subalpine fir and occasionally lodgepole pine (*Pinus contorta* Dougl. ex Loud.) are present in spruce-fir stands and contribute to overall stocking.

Knowledge is lacking of (1) the frequency of good seed crops and the kinds of stands or trees that produce good spruce crops in the uncut stands around the perimeter of openings; (2) the distance viable seeds are dispersed from the seed source into openings; and (3) the number of sound seeds required for an acceptable level of stocking in relation to seedbed, environmental, biotic, and management factors. This information is essential if proper decisions are to be made concerning the size of opening that will restock naturally, kind and amount of seedbed preparation, and whether to plant instead of depending on natural regeneration or to require the use of partial cutting methods that provide a seed source on site.

Past studies of Engelmann spruce seedfall in the Rocky Mountains indicate that intervals between good to bumper seed production years are erratic, with more poor than good seed crops (Alexander 1969, 1974; Jones 1967; Noble and Ronco 1978). The pattern of seed dispersal into clearcut openings observed in the Rocky Mountains is strongly influenced by the direction of prevailing winds. Sound seedfall generally decreases rapidly from within the stand to the stand edge, and beyond into the clearcut opening. In these studies, about 50% of the amount of seed falling under uncut stands was dispersed as far as 100 feet into the opening from the windward stand edge, and about 10% dispersed as far as 300 feet. The initial rapid decrease in seedfall was followed by a gradual tailing-off, but in the openings observed (200 to 800 feet wide), a U-shaped pattern of seedfall was poorly defined. Minimum seedfall—less than 5% of the seed falling under uncut stands—usually occurred about two-thirds of the way (150 to 600 feet) across the openings from the windward stand. Seedfall then increased, but at the leeward stand edge it was only about 30% of the sound seedfall along the windward edge (Alexander 1969, Noble and Ronco 1978, Roe 1967, Roe et al. 1970).

Past research and observations of spruce germination and survival in the Rocky Mountains have most often been concerned with identifying the environmental factors limiting success (Alexander 1984, Noble and Alexander 1977). Relatively little effort has been directed toward determining the supply of Engelmann spruce seed required for an acceptable level of stocking for a particular set of site conditions. Seed:seedling ratios previously determined for spruce have been averages over a wide range of site conditions (Noble and Ronco 1978).

STUDY AREAS

Seed production data were collected from 1970 through 1984 from thirteen sample plots, 132 feet on a side, established in old-growth spruce-fir forests, on the Fraser Experimental Forest in Colorado (Alexander et al. 1986). Plots covered a range of elevations, slopes, aspects, ages of dominant trees, and site productivity (Alexander et al. 1986). Stand characteristics for each location are shown in table 1.

Seed dispersal data were collected on two areas on the Fraser Experimental Forest from 1956 through 1965, and on five areas on different national forests in Colorado from 1962 through 1971 (Alexander 1969, Alexander and Edminster 1983, Noble and Ronco 1978). Seed sources were typical, old-growth spruce-fir stands bordering the windward and leeward edges of clearcut openings 200 to 800 feet wide, oriented with their long axis at right angles to the prevailing winds. Spruces generally accounted for between 70% and 90% of the basal area of the seed source.

Field observations of seedling establishment ratios were made from 1968 through 1982, on the Fraser Experimental Forest, on two plots approximately 4.5 miles apart (Alexander 1983, 1984). One is on a north and the other is on a south aspect at about 10,500 feet elevation. Both plots are enclosed within 100- x 110-foot hardware-cloth rodent exclosures (Noble and Alexander 1975) in the center of 3.5 acre clearcut openings in spruce-fir stands. The hardware cloth generally excluded deer mice (*Peromyscus maniculatus* Wagner), red-backed voles (*Clethrionomys gapperi* Vigors), mountain voles (*Microtus montanus* Peale), western chipmunks (*Eutamias minimus* Bachman), and pine squirrels (*Tamiasciurus hudsonicus fremonti* Audubon and Bachman), but not pocket gophers (*Thomomys talpoides* Richardson) or birds that feed on tree seeds, such as the gray-headed (dark-eyed) junco (*Junco caniceps* Woodhouse) (Noble and Shepperd 1973).

The habitat type on the Fraser Experimental Forest and on two of the national forests is *Abies lasiocarpa/Vaccinium scoparium*, the most common spruce-fir habitat

Table 1.—Average stand characteristics for dominant and codominant Engelmann spruce and total trees, seed production study, Fraser Experimental Forest.

Plot number	Trees		Basal area		Diameter		Height		Live crown	
	Spruce	Total	Spruce	Total	Spruce	Total	Spruce	Total	Spruce	Total
	Number per acre		Square feet per acre		---- Inches ----		----- Feet -----		---- Percent ----	
1	64	319	84	150	15.6	9.4	79	50	74	68
2	54	249	102	176	19.2	11.8	90	58	67	66
3	88	220	139	196	17.4	12.9	62	47	72	70
4	100	320	195	306	19.1	13.4	81	59	64	61
5	95	525	94	258	13.7	9.6	68	50	62	54
6	63	345	104	197	17.5	10.3	87	55	64	60
7	65	365	107	205	17.4	10.1	88	52	71	65
8	58	286	116	193	19.3	12.0	95	59	63	62
9	90	278	105	183	14.8	10.9	85	63	55	55
10	43	283	61	145	16.6	10.1	87	54	66	65
11	35	213	72	141	19.9	11.2	100	56	74	70
12	63	293	80	182	15.6	10.8	81	57	71	67
13	74	205	150	206	19.7	13.8	99	68	66	65

type in Colorado (Hess and Alexander 1986). The *Vaccinium* union does not compete as severely with tree seedlings as do some other habitat types. The habitat types on the other three national forests were not described but understory vegetation was dominated by *Mertensia*, or *Carex* and other graminoids.

METHODS

Seed Production

Seed production was estimated from seeds collected in 10 1-square-foot seed traps randomly located within each 0.4-acre plot (fig. 1). Seed trap contents were collected one or more times each fall beginning in mid- to late September, weather conditions permitting, and again the following spring. All seeds were tested for soundness and recorded as (1) filled, or (2) partially filled or empty. Estimates of total quantities of seed produced were based on counts of filled seed only.

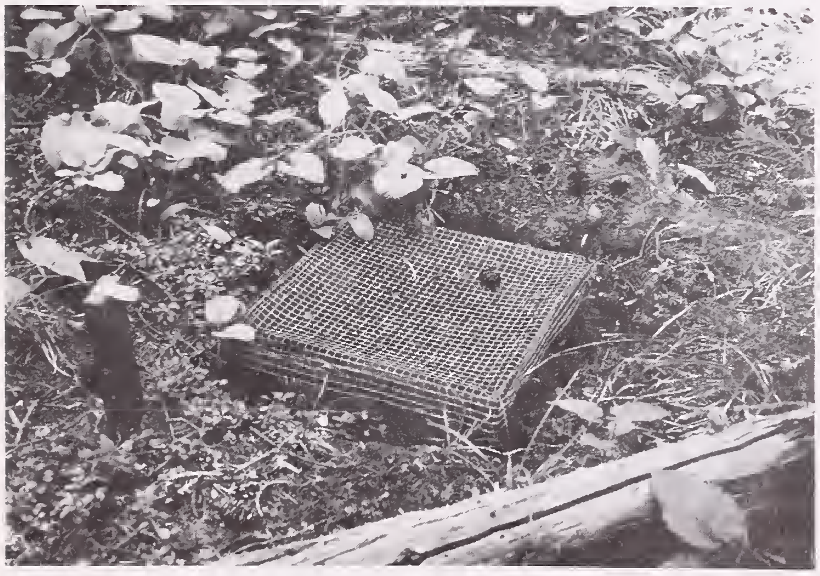

Figure 1.—One-foot-square wire seed trap in place, Fraser Experimental Forest.

Differences in seedfall for locations and years were tested by analysis of variance, with a square root transformation ($\sqrt{X + 3/8}$) of the number of filled seeds per trap as the dependent variable. Data were transformed to provide homogeneous variances.

The following subjective categories, described by Alexander and Noble (1976), were used to rate the seed crops.

Filled seeds per acre	Seed crop rating
<10,000	Failure
10,000–50,000	Poor
50,000–100,000	Fair
100,000–250,000	Good
250,000–500,000	Heavy
>500,000	Bumper

The relationship between the amount of filled seed produced and total seedfall was tested by regression analysis, with the number of filled seeds per trap as the dependent variable.

Standard stand inventory data were collected on each plot (Alexander et al. 1986). These were used to compute the usual stand, tree, and crown parameters as a basis for relating seed production to some measure of stand density, and/or crown and tree characteristics. Parameters were calculated using only dominant and codominant spruces, because numerous studies have shown that coniferous species of these crown classes produce three-fourths or more of the seedfall (Fowells and Schubert 1956, Franklin et al. 1974). A stepwise regression program was then used to select the set of independent variables best correlated with seed production.

Seed Dispersal

Seed count data were obtained from seed traps placed on transect lines. On two, 400-foot wide, clearcut areas, on the Fraser Experimental Forest, 15 3.3-square-foot (0.25 mil-acre) seed traps were placed along each of two parallel transect lines, about 132 feet apart, at right angles

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 Screen 1 of 2
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Edminster.
  9 260 0    Fort Colins, Colo. : ‡b USDA Forest Service, Rocky Mountain Forest
and Range Experiment Station, ‡c [1982]
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 11 440  0   Research note RM ; ‡v 419
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 13 500      "August 1982."
 14 504      Bibliography: p. 6.
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 18 700 10   Watkins, Ross K.
 19 700 10   Edminster, Carleton B.
 20 710 20   Rocky Mountain Forest and Range Experiment Station (Fort Collins,
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to the windward stand edge. Seed traps on each transect line were placed at 33-foot intervals, beginning 33 feet into the uncut stand along the windward stand edge and ending 33 feet into the leeward stand edge.

In the other five clearcut areas, 1-foot-square seed traps were placed on transect lines that were parallel to the long axis of the clearing. Ten seed traps were placed on each transect line, at 33-foot intervals. Transect lines were 66 feet apart, with the outer two transect lines 33 feet from the windward and leeward stand edges. One additional transect line was placed 66 feet inside both the uncut windward and leeward stands.

Seed trap contents were collected annually. Sound seed counts (based on cutting tests) were tabulated by trap on each area for each year of observation.

The relationship between mean seedfall and distance from source was explored by plotting the number of sound seeds falling from the windward stand edge into the opening (for a distance as far as seedfall appeared to be uninfluenced by the leeward stand) against the number of sound seeds falling under the uncut windward stand, which was the source of most of the seedfall in the openings. A nonlinear least squares regression program was then used to fit the data to an exponential model.

Seedling Establishment

Four seedbed treatments were tested in a two- by two-factorial, replicated over 10 years time, in randomized blocks. A set of twelve 0.25 mil-acre seedbeds (four seedbed treatments, replicated three times) were prepared on each aspect, each year from 1968 through 1977. The four seedbed treatments were (1) scarified-shaded, (2) scarified-unshaded, (3) unscarified-shaded, and (4) unscarified-unshaded (Alexander 1983, 1984; Noble and Alexander 1977). Plots were scarified by hand to remove all organic material to mineral soil. Scarification simulated scalping with a dozer blade. Wooden frames made from 2-inch wide furring strips with alternate 2-inch spaces, elevated 8 to 10 inches above the ground on metal framing, provided overhead shade (fig. 2). Slats of the shade frames were oriented in a north-south direction to provide alternate periods of shade and sunlight.

The Engelmann spruce seed used in this study was collected locally. New collections were made only when stored seed viability dropped to less than 60%. In late September of each year (1968 to 1977), an estimated 125 viable seeds were evenly broadcast on each seedbed. The total number of seeds sown per seedbed each year varied from 165 to 210, depending on viability determined from laboratory germination tests. The seeds were not covered, because the intent was to simulate natural regeneration. The number of seeds sown corresponds to 500,000 sound seeds per acre, which can be expected from a heavy natural seedfall. Plots were located at least 150 feet from the nearest timber edge to minimize the input of seed from adjacent timber stands. However, the seed: seedling ratios calculated should be considered minimums, especially because they are extrapolated from a heavy seedfall production.

Figure 2.—Shade frame in place on a scarified-shaded seedbed, Fraser Experimental Forest.

During the first growing season after each sowing, germination, survival, and mortality were recorded at least twice weekly; after the first growing season, counts were made weekly. Measurements were begun in mid-June, when the plots were first clear of snow, and ended about mid-October, with the onset of winter snow cover.

RESULTS AND DISCUSSION

Seed Production

Seed was produced in larger quantities and at more frequent intervals than previously measured on the Fraser Experimental Forest (Alexander 1969) and elsewhere in the central Rocky Mountains (Alexander 1974, Noble and Ronco 1978), as values below, averaged over all Fraser locations, show:

Year	Number of sound seeds per acre in thousands
1970	342
1971	208
1972	281
1973	19
1974	271
1975	193
1976	15
1977	1,114
1978	96
1979	13
1980	682
1981	34
1982	8
1983	82
1984	8

Based on this average seed production, crops were rated as shown for the 15 years of record.

Seed crop rating	Number of years
Failure	2
Poor	4
Fair	2
Good	2
Heavy	3
Bumper	2

There were differences in the quantity of seed produced from year to year. During the first 5 years of observation, good to heavy seed crops were produced in 4 out of 5 years. During the second 5 years, good to bumper crops were produced in 2 years; but in the last 5 years, good to bumper crops were produced in only 1 year (fig. 3). Seed crops also varied considerably between locations. Not all locations produced good to bumper crops every good seed year, and some locations produced bumper crops in 3 or more years. Analysis of variance of the seed count data revealed that differences between years, locations, and the years-times-locations interaction were all highly significant ($p \leqslant 0.01$).

The amount of filled seed for each year at each location was related significantly to the annual total seedfall, as shown in the following equation:

$$Y = 0.499\ X \qquad [1]$$

$R^2 = 0.87$, $S_{y.x} = 157{,}000$ (coefficient of determination not centered about the mean—zero-intercept model)

where

Y = number of filled seeds per acre per year, and
X = number of total seeds per acre per year.

The equation, which accounts for 87% of total variation in sound seed production, shows that the number of filled seed produced increases linearly with total seedfall. The large standard error of estimate also indicates considerable variability in the relationship between filled and total seed production between years and locations.

Another significant finding in this study is that despite good or better seed production in 7 years, an average of only 46% (range 26% to 68%) of the total seedfall collected were filled in those years. Seed loss to insects, in particular to the spruce seed worm (*Cydia youngana*), accounted for a large portion of the unsound, partially filled seeds (Schmid et al. 1981).

Regression analyses of seed production and stand inventory variables resulted in the following equations:

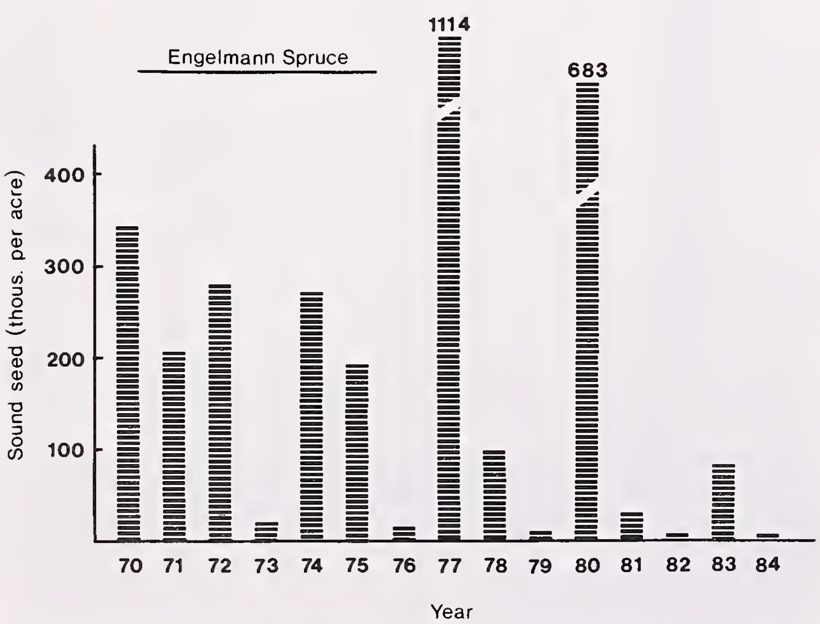

Figure 3.—Average Engelmann spruce sound seed production in relation to years.

$$Y = 5{,}395\ X^{0.796} \qquad [2]$$

$$S_{y.x} = 87{,}600$$

where

Y = periodic average annual sound spruce seed production per acre, and
X = basal area of dominant and codominant spruces per acre.

$$Y = 5{,}936\ (X_1\ X_2)^{1.217} \qquad [3]$$

$$S_{y.x} = 84{,}000$$

where

Y = periodic average annual sound spruce seed production per acre,
X_1 = average height of dominant and codominant spruces, and
X_2 = average number of stems of dominant and codominant spruces per acre.

The relationships of seed production to stand variables in both equations are weak (only 30% to 40% of the variation is accounted for), but no improvement was possible using other combinations of stand variables. However, the standard errors of estimate appear reasonable for this kind of data.

The average annual seed production was used as the dependent variable, because it is difficult to account for annual variation. Furthermore, the independent variables did not change significantly from year to year.

Seed Dispersal

The following equation was used to fit the seed dispersal data by a nonlinear least squares regression program.

$$SD = SO\ \exp[-b_1(D + 33)b^2] \qquad [4]$$

where

SD = Number of sound seeds per acre falling at distance D into the openings (the windward stand edge is denoted by $D = 0$),
SO = number of sound seeds per ha falling under the uncut stand 33 feet from the windward stand edge (denoted by ($D = -33$),
D = distance in feet into the opening from windward stand edge, and
b_1, b_2 = partial coefficients of SO and D, respectively.

The estimated value of b_2 was nearly 1.0; therefore, the following simplified model was then fit:

$$SD = SO\ \exp[-b_1(D + 33)]. \qquad [5]$$

The residual sums of squares of the two models were nearly equal. The resulting equation from the single coefficient model is:

$$SD = SO\ \exp(-0.00735D - 0.243) \qquad [6]$$

$R^2 = 0.99$, $Sy{:}x = 37{,}500$ sound seeds per acre.

Although the equation accounts for 99% of the variability centered about the mean, the high standard er-

ror of estimate indicates that a large amount of variability is not accounted for by the equation.

The precision of equation [6] is about the best that can be expected for estimating seedfall in relation to seed production and distance from source because of the variation in seedfall from year to year and from place to place. More data are not likely to reduce the large standard error of estimate (Alexander and Edminster 1983).

Equation [6] is useful in estimating potential Engelmann spruce seedfall into openings in the central Rocky Mountains. Figure 4 was developed from equation [6] to estimate seedfall into openings for distances up to 600 feet from the windward stand edge. Seed production under uncut stands was set at a range of 50,000 to 1,000,000 sound seeds per acre.

Estimates of seedfall into openings generally follow the pattern previously described for the Rocky Mountains. The amount of seedfall dispersed to the windward stand edge is about 80% of the seedfall under the uncut stand. About 40% of the amount of seedfall under the uncut windward stand is dispersed as far as 100 feet, and about 10% as far as 300 feet. The rapid decline in seedfall then levels off, with about 1% of the amount of seed falling under uncut stands dispersed as far as 600 feet from the windward stand edge. This is in general agreement with the 0.5% to 5% estimates of seedfall at 600 feet from source observed by Roe (1967). There are two important differences, however: equation [6] is based on estimates of sound seed, not total seedfall, and on two 10-year periods of observation.

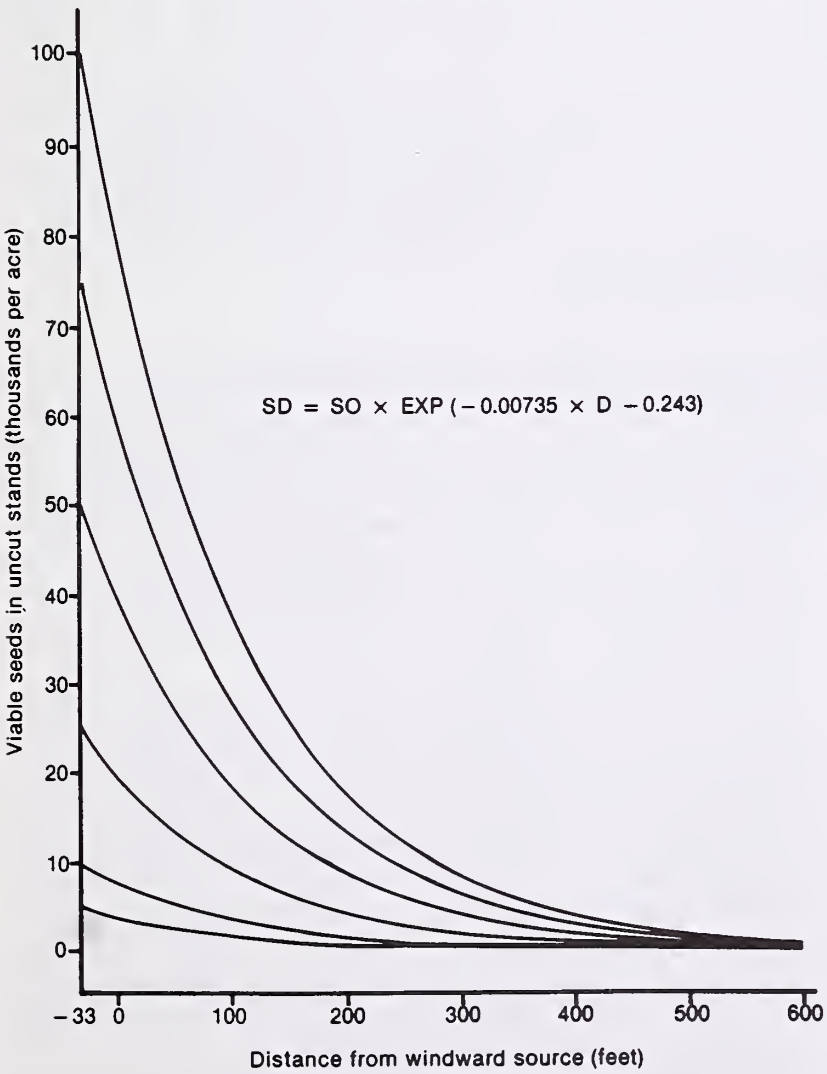

Figure 4.—Seed dispersal in relation to seed production in uncut stands and distance from source (estimated from equation [6]).

Seedling Establishment

Germination

Germination was considerably better on the north aspect than on the south aspect (table 2). However, total germination on the north aspect for all years was only 6.1%, ranging from a high of 10.5% in 1974 to a low of 0.9% in 1971 (table 2). Germination was improved significantly in most years by scarification but not by shade. The scarification x years interaction was highly significant, indicating that there was considerable variability in germination from year to year on scarified seedbeds (Alexander 1984).

Total germination for all years on the south aspect was only 2.9%, ranging from a high of 14.5% in 1972 to a low of 0.2% in 1970 (table 2). In some years, shade significantly improved germination, and in a few years, the combination of shade and scarification significantly improved germination. All interactions between years and cultural treatments were highly significant, indicating high variability in germination among the treatments from year to year (Alexander 1984).

Survival

Survival also was better on the north aspect than on the south aspect (table 2). However, total survival on the north aspect at the end of the study was only 1.4% of the viable seeds sown. Seedlings that survived through the fifth growing season generally survived to the end of the study. In most years, survival was significantly improved by scarification, by shade, and by the combination of scarification and shade. The scarification x years interaction and the differences in survival between years also were significant (Alexander 1984).

On the south aspect, total survival was only 0.2% of the viable seeds sown (table 2). Although seedlings that survived through the fifth growing season generally survived to the end of the study, there was no survival on any of the seedbed treatments for seeds sown after 1975. In those few years when seedlings survived beyond the first year, shade and the combination of shade and scarification significantly improved survival. The shade x years interaction was significant, indicating high variability between years (Alexander 1984).

Mortality

Seventy-six percent of the seedlings that germinated on the north aspect died by the end of the study. About two-thirds of the total mortality occurred the first year (table 3). On the south aspect, 95% of the seedlings were

Table 2.—Percent germination and survival of Engelmann spruce by aspect, seedbed treatment, and year (basis number of viable seeds sown) (Alexander 1984).

	Scarified and shaded				Scarified and shaded				Unscarified and shaded				Unscarified and unshaded				Total			
	Germ-	Survival end of			Germ-	Survival end of			Germ-	Survival end of			Germ-	Survival end of			Germ-	Survival end of		
Year	ination	1st	5th	study[1]	ination	1st	5th	study[1]	ination	1st	5th	study[1]	ination	1st	5th	study[1]	ination	1st	5th	study[1]
										North aspect										
1969	21.1	10.9	7.5	6.9	12.8	7.2	3.2	3.2	4.5	1.6	1.3	0.8	0.8	0	0	0	9.8	4.9	3.0	2.7
1970	12.5	8.8	4.5	4.3	7.2	4.3	1.6	1.6	4.5	2.1	0.3	0.3	1.3	0.5	0.5	0.5	6.4	3.9	1.8	1.7
1971	1.1	0.5	0.5	0.5	2.1	2.1	0.5	0.5	0	0	0	0	0.5	0.3	0	0	0.9	0.7	0.3	0.3
1972	6.9	1.3	0.8	0.8	11.2	0.8	0	0	1.6	0.3	0	0	2.4	0.3	0	0	5.5	0.7	0.2	0.2
1973	7.2	4.0	2.1	2.1	3.5	1.3	0.3	0.3	9.6	5.9	3.5	2.9	3.2	1.9	0	0	5.9	3.3	1.5	1.3
1974	8.0	5.9	2.9	2.7	2.1	1.1	0.3	0.3	21.1	4.5	2.4	2.1	10.9	2.1	0.5	0.5	10.5	3.4	1.5	1.4
1975	9.3	3.7	0.5	0.5	8.3	3.7	0.5	0.5	4.8	2.9	1.6	1.3	1.1	0.5	0	0	5.9	2.7	0.7	0.6
1976	1.6	0.5	0.3	0.3	1.1	0.5	0.3	0.3	8.3	5.9	2.9	2.9	2.1	1.9	1.3	1.3	3.3	2.1	1.2	1.2
1977	10.7	8.3	2.4	2.4	4.8	2.4	0.3	0.3	1.3	1.1	0.3	0.3	1.1	0.5	0	0	4.5	3.1	0.7	0.7
1978	15.2	10.9	9.9	9.9	11.7	7.2	6.1	6.1	4.5	2.9	1.6	1.6	0.3	0	0	0	7.9	5.3	4.4	4.4
Aver.	9.4	5.5	3.1	3.0	6.5	3.1	1.3	1.3	6.0	2.7	1.4	1.2	2.4	0.8	0.2	0.2	6.1	3.0	1.5	1.4
										South aspect										
1969	6.7	1.3	0.3	0.3	2.1	0	0	0	6.9	2.4	1.9	1.9	2.4	0	0	0	4.5	0.9	0.5	0.5
1970	0	0	0	0	0	0	0	0	0.8	0.3	0.3	0.3	0	0	0	0	0.2	0.1	0.1	0.1
1971	1.6	0.5	0.5	0.5	1.3	0	0	0	0.3	0	0	0	0.5	0	0	0	0.9	0.1	0.1	0.1
1972	10.9	1.9	0.8	0.8	9.6	0.5	0	0	26.9	1.1	0	0	10.7	0	0	0	14.5	0.9	0.2	0.2
1973	5.9	2.4	1.3	1.3	0	0	0	0	5.9	2.4	1.1	0.5	2.7	1.3	0	0	3.6	1.5	0.6	0.5
1974	0	0	0	0	0	0	0	0	5.6	0.3	0	0	5.1	0	0	0	2.7	0.1	0	0
1975	0.3	0	0	0	0	0	0	0	0.8	0	0	0	0	0	0	0	0.3	0	0	0
1976	0.3	0	0	0	0	0	0	0	0.8	0.3	0	0	0	0	0	0	0.3	0.1	0	0
1977	2.7	0.3	0	0	0	0	0	0	4.3	0.3	0	0	0	0	0	0	1.7	0.1	0	0
1978	0.5	0	0	0	0.5	0	0	0	0.5	0	0	0	0	0	0	0	0.4	0	0	0
Aver.	2.9	0.6	0.3	0.3[2]	1.4	0.1	0	0	5.3	0.7	0.3	0.3	2.1	0.1	0	0	2.9	0.4	0.2	0.2

[1] *Seedling age in 1982 ranged from 5 years old (1978 germination) to 14 years old (1969 germination).*
[2] *Seedling age in 1982 ranged from 10 years old (1973 germination) to 14 years old (1969 germination).*

dead by the end of the study, with more than 90% of the total mortality occurring the first year (Alexander 1984).

Drought was the most significant cause of mortality on both aspects, followed by clipping by birds (table 4). On the north aspect, these two factors plus frost heave and snowmold accounted for nearly 90% of the mortality. On the south aspect, drought, clipping, and heat girdle accounted for about 90% of the mortality (Alexander 1984).

Seed:Seedling Ratios

The lowest seed:seedling ratios were on the scarified-shaded seedbeds, on the north aspect, where treatment was most effective in conserving moisture by lowering temperatures of both soil and seedlings, and reducing competing vegetation (Alexander 1983).

Neither shade nor scarification was as effective in conserving moisture as the combination of shade and scarification on the north aspect; fewer seeds germinated and fewer seedlings survived on the scarified-unshaded and unscarified-shaded seedbeds. Survival stabilized on all treated seedbeds by the fifth growing season, but it required nearly 2.5 times as many seeds to produce a 5-year-old seedling on the scarified-unshaded and unscarified-shaded seedbeds as on the scarified-shaded seedbeds. The highest seed:seedling ratios on the north aspect were on unscarified-unshaded seedbeds. Thirteen times as many seeds were required to produce a 5-year-old seedling as on scarified-shaded seedbeds (Alexander 1983) (table 4).

On the south aspect, the lowest seed:seedling ratios were on the scarified-shaded and unscarified-shaded seedbeds. Seed:germinating seedling ratios were higher on the unscarified-shaded seedbeds, but first-year survival was lower. Seedling survival stabilized by the fifth growing season on these seedbeds, but compared to comparable seedbed treatments on the north aspect, it required more than 10 times as many seeds on scarified-shaded seedbeds, and nearly 5 times as many on the unscarified-shaded seedbeds to produce a 5-year-old seedling (Alexander 1983) (table 4).

Few seeds germinated and no seedlings survived as long as five growing seasons on either the scarified-unshaded or unscarified-unshaded seedbeds on the south

Table 3.—Percent total mortality by aspect, cause, and seedbed treatment (basis number of seedlings that germinated) (Alexander 1984).

Cause of mortality	Scarified-shaded			Scarified-unshaded			Unscarified-shaded			Unscarified-unshaded			Total		
	End 1st yr	End 5th yr	End study[1]	End 1st yr	End 5th yr	End study	End 1st yr	End 5th yr	End study	End 1st yr	End 5th yr	End study	End 1st yr	End 5th yr	End study
North aspect															
Drought	9.9	14.2	14.2	8.3	9.9	9.9	15.6	20.2	20.5	7.8	10.4	10.4	41.6	54.7	55.0
Clipping	7.2	7.2	7.2	6.1	6.1	6.1	1.3	1.3	1.3	0	0	0	14.6	14.6	14.6
Frost heave	0.3	6.4	6.4	0.6	4.5	4.5	0.1	0.7	0.7	0	0.5	0.5	1.0	12.1	12.1
Snowmold	0	0.9	1.3	0	2.6	2.6	0	0.7	1.2	0	0	0	0	4.2	5.1
Washout	2.0	2.3	2.3	1.0	1.2	1.2	0	0	0	0	0	0	2.9	3.5	3.5
Freezing	0.1	0.1	0.1	0.1	0.1	0.1	0.4	0.7	0.7	0.7	0.7	0.7	1.1	1.6	1.6
Heat girdle	0.7	0.7	0.7	0.9	0.9	0.9	0.1	0.1	0.1	0	0	0	1.7	1.7	1.7
Other[2]	0.9	1.9	2.0	1.4	2.5	2.5	0.6	1.8	1.9	0	0	0	2.9	6.2	6.4
Total	21.0	33.7	34.2	18.3	27.8	27.8	18.1	25.5	26.4	8.5	11.6	11.6	65.8	98.6	100.0
South aspect															
Drought	10.1	11.1	11.1	7.7	7.7	7.7	23.8	26.0	26.5	13.9	14.7	14.7	55.5	59.5	60.0
Clipping	7.0	7.0	7.0	0.5	0.5	0.5	10.8	10.8	10.8	1.2	1.2	1.2	19.5	19.5	19.5
Frost heave	0.5	2.2	2.4	0.5	0.9	0.9	0.5	0.5	0.5	0	0	0	1.5	3.6	3.8
Snowmold	0	0	0	0	0	0	0	0.2	0.2	0	0	0	0	0.2	0.2
Washout	1.2	1.2	1.2	0.7	0.7	0.7	0	0	0	0	0	0	1.9	1.9	1.9
Freezing	0	0.2	0.2	0	0	0	0.5	0.5	0.5	0	0	0	0.5	0.7	0.7
Heat girdle	1.0	1.0	1.0	1.7	1.7	1.7	4.8	4.8	4.8	2.6	2.6	2.6	10.1	10.1	10.1
Other[3]	0.2	0.5	0.5	0.7	0.7	0.7	1.0	1.9	1.9	0.7	0.7	0.7	2.6	3.8	3.8
Total	20.0	23.2	23.54[4]	11.8	12.2	12.2	41.4	44.7	45.2	18.4	19.2	19.2	91.6	99.3	100.0

[1]*Seedlings age at end of study (1982) varied from 5 to 14 years old.*
[2]*Includes isolation, damping off, gophers, and unknown.*
[3]*Includes isolation, damping off, and unknown.*
[4]*Seedlings age at end of study (1982) varied from 10 to 14 years old.*

Table 4.—Seed to seedling ratios at the end of germination, and the fifth growing seasons by seedbed treatment and aspect.

Aspect	Seedbed treatment	Germinating seedlings		Fifth year survival[1]	
		Mean	Range	Mean	Range
N	Scarified shaded	11:1	5:1 to 94:1	32:1	10:1 to 375:1
	Scarified unshaded	15:1	8:1 to 94:1	76:1	16:1 to ∞
	Unscarified shaded	17:1	5:1 to ∞[1]	72:1	29:1 to ∞
	Unscarified unshaded	42:1	9:1 to 375:1	417:1	75:1 to ∞
S	Scarified shaded	35:1	9:1 to ∞	341:1	75:1 to ∞
	Scarified unshaded	74:1	10:1 to ∞	∞	
	Unscarified shaded	19:1	4:1 to 375:1	312:1	54:1 to ∞
	Unscarified unshaded	46:1	9:1 to ∞	%	

[1]∞ = *no germination or survival.*

aspect (table 4). Germination was low because seedbeds were too cold immediately after snowmelt, and by the time they were warm enough for seedlings to emerge, the seedbeds were too dry. Moreover, water losses from soil and seedlings were so great that reducing air and soil temperatures by shading to conserve moisture was absolutely essential to any survival, regardless of the seedbed (Alexander 1983).

At age 5 years, 800 seedlings per acre is a reasonable stocking goal for Engelmann spruce (Alexander and Edminster 1980). This is more than required for adequate stocking, but necessary to achieve uniform spacing, allow for possible future mortality, and provide options in selecting crop trees in subsequent thinnings. Numbers of seeds, based on seed to 5-year-seedling ratios in table 4, required to produce this stocking level under different seedbed conditions on north and south aspects are shown in table 5.

Seed data presented in tables 4 and 5 are minimums, based upon the exclusion of seed-eating small mammals, but not birds that consume tree seeds. All spruce-fir forests support populations of these small mammals, and any disturbance that initiates understory plant succession probably favors a buildup of these populations, particularly if slash and other downed materials are present to provide cover. Although these mammals consume considerable seed, the magnitude of losses to them is not known in the central Rocky Mountains. It seems reasonable to expect that under poorest conditions in the central Rocky Mountains, losses could be as high as 50% of the viable seed produced in a good seed year.

RECOMMENDATIONS

Equations [2] and [3] are useful for estimating potential periodic annual spruce seed production in stands with different characteristics, but the standard errors of estimate approximated from the untransformed residuals are very high. Therefore, the resolution between poor to heavy seed crops is not very good. These equations also do not provide the means for estimating the seed

Table 5.—Number of viable seeds required to produce 800 5-year-old Engelmann spruce seedlings per acre in relation to seedbed treatment and aspect.[1]

Seedbed treatments	Aspect	
	North	South
Scarified shaded	25,600	272,800
Scarified unshaded	60,800	∞[2]
Unscarified shaded	57,600	249,600
Unscarified unshaded	333,000	∞

[1]*Data presented are based upon the exclusion of seed-eating mammals. If these animals are not excluded, numbers of seed required should be increased by 100%.*

[2]*∞ = no survival.*

crop rating for any individual year. In some years, seed crops will be total failures, and, even in years of good overall seed production, not all locations will produce good to bumper seed crops.

Figure 4 is useful in approximating Engelmann spruce seedfall into clearcut openings. However, while the curves developed from equation [6] fit the trends in seed dispersal very well, there is considerable variability around the curves. This means that estimates of seedfall for an individual year at any location may vary considerably from actual seedfall.

The data presented in tables 4 and 5 were derived from one habitat type at one location, the Fraser Experimental Forest. In the absence of better information, they can be used to approximate what might occur on similar seedbeds in this habitat type elsewhere. However, while the viability of seed used in this study was good, the criterion that 125 viable seeds be sown on each seedbed each year was based on laboratory germination tests. Actual viability in the field, therefore, may have been lower, in which case the seed:seedling ratios are too low. Small mammals that consume tree seed were excluded from the seedling study, but exclosures suitable for research purposes are not practical for operational timber sales. The effectiveness of other rodent abatement procedures, such as treating seed or baiting, is not known for spruce-fir forests in the central Rocky Mountains. Moreover, little is known about seed predation by small mammals in spruce-fir forests. Estimates of possible losses to seed-eaters are highly speculative, therefore. Seed:seedling ratios vary considerably with climatic changes. These data cover a period of time 1968 to 1982, but represent only the weather conditions during that period. The distribution of summer precipitation varied more than the amount. Summer rainfall was more erratic during the period 1974 through 1980 than either before or after. No seedlings that germinated after 1973 survived on the south aspect (Alexander 1984).

In estimating the size of clearcut opening likely to restock naturally within a 5-year period, the following assumptions were made based on the data presented.

1. Accumulative production of 500,000 to 1,000,000 sound seeds per acre in uncut stands over a 5-year period is not an unreasonable expectation.
2. Fifty percent of the viable seeds produced will be lost to seed-eaters.
3. At age 5 years, 800 seedlings per acre is a desirable stocking goal.
4. Figure 4 is a reasonable estimate of the distance seed is dispersed from source.

On north aspects, the effective seeding distance on scarified-shaded seedbeds is about 200 to 350 feet from the windward stand edge. Openings 300 to 450 feet wide (assuming an effective seeding distance of 50 to 100 feet from the leeward stand edge) should adequately restock within 5 years. The effective seeding distance on scarified-unshaded and unscarified-shaded seedbeds on the north aspect is about 150 to 250 feet from the windward stand edge, with openings 200 to 350 feet wide restocking adequately within 5 years. On unscarified-unshaded seedbeds on the north aspect, and all seedbeds

on the south slope, the effective seeding distance is so limited that clearcutting, with the expectation of adequate natural restocking in a reasonable period of time, is not a viable option. Under these conditions, a shelterwood cutting method is recommended for even-age management with natural reproduction.

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Engelmann spruce seed production and dispersal, and seedling establishment in the central Rocky Mountains indicate that in the *Abies lasiocarpa/Vaccinium scoparium* habitat type, shaded, mechanically scarified, mineral soil seedbeds on north aspects can be adequately restocked naturally within a 5-year period in clearcut openings 300 to 450 feet wide. With shade or scarification alone, size of opening that will restock is reduced to 200 to 350 feet. The effective seeding distance is so limited on unshaded natural seedbeds on north aspects and on south aspects regardless of the seedbed conditions that the expectation of natural restocking in a reasonable period of time with clearcutting, is not a realistic option.

Keywords: *Picea engelmannii*, natural forest regeneration

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Rocky Mountains

Southwest

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